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Summary.—New Guinea's mountains consist today of the high Central Range, plus ten isolated lower outlying ranges. But during Pleistocene periods of low sea level, when New Guinea's current shallow continental shelf was exposed as dry land, the main island included further outliers that subsequently became cut off as land-bridge islands as rising sea levels submerged the shelf connecting them to New Guinea. We surveyed the upland avifauna of Yapen, the highest of those land-bridge islands. Yapen supports 26 upland species. That number is higher than on nearby oceanic islands of similar elevation, because Yapen in contrast to oceanic islands could acquire species overland during the Pleistocene. However, that number is much lower than on New Guinea's outliers of similar elevation, due to extinctions of many of Yapen's populations following its isolation as an island.

Of New Guinea's 193 upland species, some are much more widely distributed on the ten outliers than the rest. Yapen's upland species, and those of the other land-bridge islands, are a small subset of those successful colonists of mainland outliers. Part of the explanation for differential success is that only species whose elevational floors lie well below the summits of the outliers and of Yapen are likely to have survived on or colonised those mountains, all much lower than New Guinea's Central Range. For the remainder, we infer that more than half of Yapen's former upland populations have gone extinct since Yapen's isolation. For those species with poor ability to disperse overwater, abundance is a predictor of survival and continued presence on Yapen—as expected from the inverse relationship between extinction risk and population size.

We identify half-a-dozen mechanisms for colonisation by upland species: dispersal overwater when Yapen was an island; regular post-breeding descent to the lowlands; irregular straggling to the lowlands; dispersal through flat lowlands; dispersal over hill bridges; and dispersal during cool Pleistocene phases, when some current upland species had lowland populations. Relict sets of those mostly vanished Pleistocene lowland populations survive on three remnant fragments of southern New Guinea's former Arafura platform: on the Aru Islands, New Guinea's Fly River bulge, and the northern tip of Australia's Cape York Peninsula.

We report here four explorations and an analysis of the upland avifauna of Yapen Island, 21 km off the north coast of western New Guinea. (By upland avifauna, we mean species largely confined to sloping elevated terrain, and absent from the level-ground lowlands at or near sea level, as discussed below.) Yapen is one of the six large land-bridge islands on New Guinea's continental shelf (Fig. 1). That is, the ocean waters separating Yapen from New Guinea today are sufficiently shallow that they became dry land at Pleistocene times of low sea level, and Yapen then formed a northern extension of the New Guinea mainland (Beehler 2007). At that time, animal and plant species unable or reluctant to cross water, and that currently cannot reach Yapen overwater, were able to reach it overland. Those

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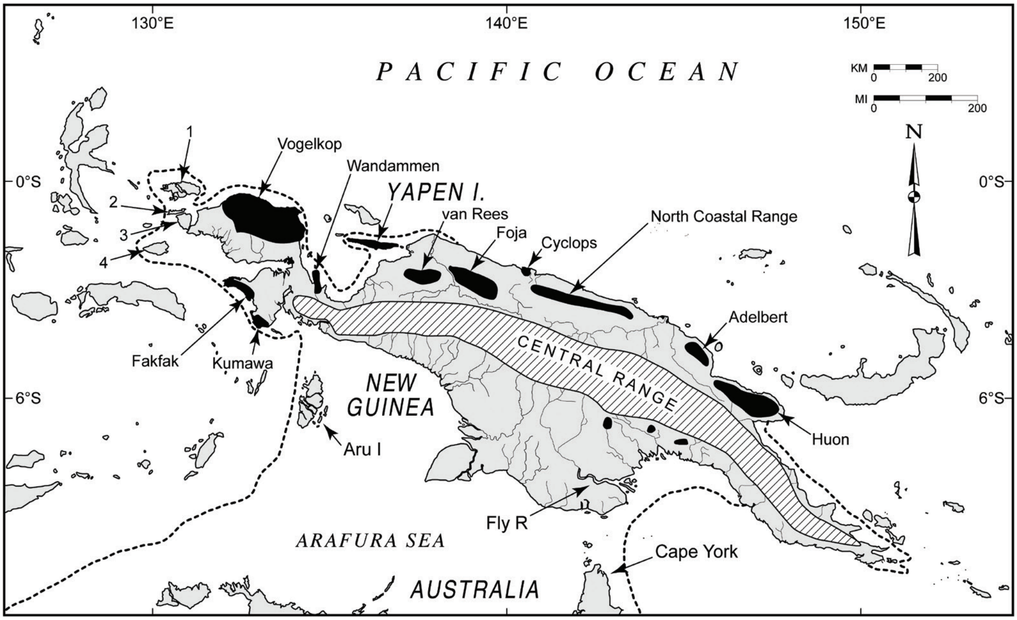

Figure 1. New Guinea (modified from Fig. 1 of Diamond & Bishop 2015), showing Yapen Island, the five other large land-bridge islands, and the main mountain ranges. The dashed line marks the limits of the New Guinea continental shelf. During Pleistocene times of low sea level, the shelf, which is now a shallow sea, was a dry-land extension of the New Guinea mainland, and Yapen and other large land-bridge islands formed part of the New Guinea mainland. The current Arafura Sea was then a large exposed lowland platform, of which the modern fragments are the Aru Islands, New Guinea's Fly River bulge, and the north tip of Australia's Cape York Peninsula. Islands: 1–4 = West Papuan Islands (1 = Waigeo, 2 = Batanta, 3 = Salawati, 4 = Misool). New Guinea's mountains are the Central Range (cross-hatched) and the ten outlying ranges on New Guinea's north and north-west coasts.

non-water-crossing species include the majority of New Guinea bird species, especially forest interior and upland species (Diamond 1972a), which avoid crossing water or forest clearings although perfectly capable of flight. When rising sea levels at the end of the Pleistocene flooded the land bridge and Yapen became an island, the Yapen populations of those non-water-crossing species became isolated, and many of those inferred former populations are now absent and presumed to have disappeared (Diamond 1972a).

As the highest of New Guinea's land-bridge islands (1,430 m), Yapen has the richest upland avifauna, currently known to comprise 26 species. That Yapen upland avifauna is interesting for at least four reasons. First, some of its inferred bird populations have survived, and many others evidently have not. What factors influenced that differential survival of bird populations in isolation?

Second, the mountains of the New Guinea mainland consist of the 5,000 m-high Central Range, extending 2,400 km west to east, plus ten isolated small ranges rising from the lowlands along the north and north-west coast (Fig. 1). Of the approximately 193 upland bird species or superspecies of the Central Range, some occur on all ten of the outliers, some on various but not all outliers, and some on none. What accounts for these great differences in mountain colonisation among New Guinea's upland species? Because five of the six large land-bridge islands (including Yapen) are high enough to support upland species and were formerly part of the New Guinea mainland, they add to the database for answering this question about mountain colonisation.

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Third, most of the mainland outliers are joined or nearly connected to the Central Range or to another outlier by low hills. But two of the outliers, the Fakfak Mts. and Kumawa Mts., are isolated from the nearest hilly terrain of the Central Range by 70–100 km of entirely level-ground lowlands almost at sea level. The Fakfak and Kumawa Mts. lack 15 upland species present on other outliers, and for which the Fakfak and the Kumawa Mts. lie within the elevational and geographic ranges of the species (Diamond & Bishop 2015). A possible explanation is that those upland species disperse overland through forest on low-elevation undulating terrain, but not through forest on flat terrain at sea level. When Yapen was part of the New Guinea mainland during Pleistocene periods of low sea level, the terrain that separated it from the nearest other New Guinea mountains was also level-ground terrain at sea level. Thus, Yapen's upland avifauna offers a test of the hypothesis that certain upland bird species do not disperse through flat lowland forest.

Finally, one can postulate at least six different mechanisms by which upland species might disperse between isolated blocks of suitable habitat. Yapen's upland avifauna may help to evaluate the relevant importance of those different mechanisms.

At the outset, we must dampen the expectations of readers hoping for unequivocal answers to those questions. We could obtain answers at high levels of statistical significance if the New Guinea region included hundreds each of ornithologically well-explored outlying mountain ranges, land-bridge islands, and oceanic islands of various areas and elevations, variously separated by hilly or flat terrain. But the New Guinea region offers only ten outliers and six large land-bridge islands, and only two of the outliers are isolated by level-ground terrain. Furthermore, Yapen is distinctive for two separate reasons, making it not straightforward to separate the contributions of those two factors: Yapen is currently a land-bridge island rather than a mainland outlier, and it was formerly isolated by flat rather than by hilly terrain. Furthermore, there is no fossil evidence to prove which bird species actually inhabited Yapen at Pleistocene times of low sea level; we are currently forced to rely on inference. Therefore, our tentative conclusions will require further testing, e.g., by fossil, molecular phylogenetic and population genetic evidence.

Natural environment

Yapen's area of 2,230 km^2 makes it the third largest of New Guinea's six large land-bridge islands, smaller than Aru or Waigeo, but larger than Misool, Salawati or Batanta. The island is long and narrow, 166 km from west to east, but only 26 km north to south at the widest point in the island's centre. Yapen's central mountain chain also runs west–east and comprises two sections: a slightly lower western section almost due north of the coastal town of Serui, and a slightly higher eastern part. Maps give the summit elevations as 1,435 and 1,496 m, respectively. However, the real elevations are slightly lower; in 1983 JD determined that of the highest western peak (Mt. Aror) as 1,340 m by ascending it with a Thommen altimeter, and that of the eastern peak as 1,430 m by flying past it in clear weather in a fixed-wing airplane with an aviation altimeter. The elevations of the western and eastern peaks that KDB measured using Google Earth are 1,374 m and 1,422 m, respectively. Elevations that I. Woxvold kindly measured by NASA's Shuttle Radar Topography Mission are 1,380 and 1,450 m, respectively.

Rainfall at various sites on Yapen, from Indonesian government records and Brookfield & Hart (1966), is 3.1–3.8 m p.a. in both the northern and southern watersheds. The wetter months are January–May in the northern watershed, and June–September in the southern watershed (including at the mountain village of Ambaidiru and coastal town of Serui). However, seasonal differences in rainfall are modest: at all sites, the driest month receives only 30–50% less rainfall than the wettest.

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Yapen's mammals include many species unlikely to be able to cross water, thereby clearly demonstrating the legacy of the Pleistocene land bridge. Among them are at least three species of kangaroos and wallabies, three species each of *Echymipera* bandicoots and dasyurids (marsupial carnivores), six species of phalangers and pseudocheirids (mostly arboreal possums), and a giant rat (*Uromys* sp.), plus many species of bats and smaller rodents (Flannery 1990; K. Koopman pers. comm., T. Flannery pers. comm.).

Yapen harbours *c*.150 resident bird species, of which about 120 occur in the lowlands and 26 are upland. That avifauna includes some 13 endemic subspecies, of which the most distinctive are the Northern Variable Pitohui *Pitohui kirhocephalus jobiensis*, Tropical Scrubwren *Sericornis beccarii jobiensis*, and Lesser Bird of Paradise *Paradisaea minor jobiensis*. The avifauna reveals the legacy of Yapen's Pleistocene land bridge as clearly as does the mammal fauna, by including representatives of many New Guinea bird genera confined to the mainland and its land-bridge islands, but absent from all islands of the Papuan region not on New Guinea's continental shelf. Land-bridge relict genera present on Yapen include *Goura*, *Pseudeos*, *Probosciger*, *Melidora*, *Ptilorrhoa*, *Crateroscelis*, *Sericornis*, *Arses*, *Tregellasia*, *Peneothello*, *Pachycephalopsis*, *Pitohui*, *Toxorhamphus*, *Melilestes* and *Melanocharis*.

Tall forest, decreasing in height with increasing elevation, still covers much of Yapen. The dominant tree species that one encounters from the beach into the mountains, provisionally identified in 1983 by A. Kayoi, can be briefly summarised as follows. Along the beach one finds *Terminalia catappa*, *Barringtonia asiatica*, *Calophyllum inophyllum*, *Artocarpus* sp. and *Casuarina* sp., and immediately behind it is often a swamp of Nipa palms (*Nypa fruticans*). On coastal slopes dominant trees are *Palaquium amboinense*, *Octomeles sumatrana*, *Intsia bijuga*, *Ficus benjamina*, *Eugenia* sp. and *Artocarpus* sp. In lowland forest further inland dominant are *Palaquium amboinense*, *Octomeles sumatrana*, *Calophyllum* sp., *Terminalia* sp., *Manilkara* sp., *Pometia acuminata* and *P. pinnata*. In the mountains the main species are *Pometia acuminata*, *Cryptocarya* sp., *Tristania* sp., *Palaquium amboinense* and *Calophyllum* sp., whereas *Araucaria cunninghamii* and *Anisoptera polyandra* are patchily distributed in the uplands. At 1,340 m on the summit of Mt. Aror the forest is *c*.15 m tall, with many small ferns in the understorey, much dead leaf litter on the ground, and some moss on trunks and limbs. In second growth on sites of former gardens and landslides the dominant tree is *Albizia falcata*, which often forms almost monospecific stands. The export logging industry on Yapen used mainly *Campnosperma brevipetiolata*, *Cananga odorata*, *Palaquium amboinense* and *Intsia bijuga*, with lesser use of *Diospyros* sp., *Dracontomelon* sp. and *Artocarpus* sp. Trees felled by hand for local use consist mostly of *Intsia bijuga* and *Pometia acuminata*.

People and languages

Yapen's largest town is the government centre of Serui on the south coast, an hour's drive east of the airport linking Yapen by scheduled flights to Biak. Formerly, much of Yapen's population, now grown to 100,000 people, lived in the mountainous interior, to escape attacks by raiders from Biak. Once the risk of these attacks vanished, most people moved to the coast, attracted by stores, medical care, schools, government services, and access by ship and plane to the outside world. The only mountain villages still inhabited are Ambaidiru and nearby Mambo, inland of Serui on the southern slopes of Yapen's western peaks.

The language atlas *Ethnologue* (Lewis 2009) lists 13 native languages as spoken on Yapen. Of these, 11 belong to the widespread Austronesian language family, believed to have reached the New Guinea lowlands (mainly the north coast) from Taiwan via Indonesia around 3,500 years ago. Ten of these Austronesian languages are confined to Yapen and nearby islets; the 11th is a small population speaking the Biak language, presumably

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brought more recently by Biak raiders. Yawa and Saweru, the two other languages, are Yapen's only Papuan tongues, i.e. belonging to a language family spoken only on New Guinea and presumably representing the main island's earlier population pre-dating Austronesian arrival. Surprisingly, the only other languages thought to be related to Yawa and Saweru are six languages spoken in the far west of the Vogelkop Peninsula, 400 km west of Yapen. Yawa, Yapen's second largest language with 6,000 speakers, is the one that we encountered at Ambaidiru. Our species accounts provide Yawa language names that Ambaidiru informants volunteered for 13 of Yapen's upland bird species, which they and we encountered together at Ambaidiru.

Ornithological studies by others

In the 1800s six collectors or teams obtained bird specimens on Yapen. At the time the island was not controlled by the Dutch colonial government and was dangerous: for example, one of William Doherty's hunters was murdered, and two others attacked, during Doherty's visit of a few weeks in 1897. All of those early collectors were based on the south coast and may at most have obtained some specimens from hunters in the interior. The species that they recorded, including ten upland species, were found by us at elevations below 600 m. The material was reported by Salvadori (1880–82), by Rothschild & Hartert (1901–15), or by both. The six early collectors were H. Rosenberg in 1869; A. B. Meyer in 1873; A. A. Bruijn's hunters, sometimes with Léon Laglaize, in 1874–85; Odoardo Beccari in 1875; F. H. H. Guillemard, sometimes with Wilfred Powell, in 1883; and William Doherty in 1897.

The largest collection of Yapen birds, 106 species, was made in 1931 by Georg Stein, who was the only collector known to have reached the interior and higher elevations. He made his upper camp at an elevation of 950 m and thereby added six species to our knowledge of Yapen's upland avifauna. His collection was reported by Rothschild *et al*. (1932).

In 2019 Verhelst & Pottier (2020) camped at 1,310 m on Yapen's eastern peak, used camera traps as well as sound-recorders, observed 12 of the 23 upland species previously recorded, and added three further upland species.

Our studies

1983.—JD surveyed birds as member of a four-man team whose three other members were studying forests and environmental issues (Alexander Kayoi of the Indonesian Forestry Department, and Ardy Irwanto and Karel Rumboirusi of the Indonesian Environment Department = PPHA). JD & Irwanto arrived in Serui on 6 August. On 7–8 August JD surveyed forests, second growth, and gardens on the coast from Serui east to Kabuena village. On 9 August JD and the other three team members drove from Serui a short distance inland to Wontembu village, from where they and their porters climbed on foot all day to Ambaidiru village (640 m) by the eastern of the two tracks linking Wontembu to Ambaidiru. The latter remained the team's base until their return to Wontembu on foot on 18 August by the western trail fording the Wendanu River (680 m), then by vehicle to Serui. From Ambaidiru, JD ascended Mts. Aror (1,340 m), Muibini (1,245 m) and Mangkiniwai (915 m), and surveyed forests from those summits down to 530 m.

2016.—KDB arrived in Serui by plane on 2 December and departed on 7 December. Transport options were more extensive than in 1983: whereas in 1983 the only motor roads were on or near the coast, by 2016 a paved trans-island road had been completed from the south coast east of Serui, reaching a first crest at 720 m, dropping to a bridge over a river at 126 m, and rising to a second crest at 938 m before dropping again to the north coast.

ISSN-2513-9894 (Online)

At an elevation of 655 m along the trans-island road between the first crest and the river, an unpaved road forks left, rises to a crest at 1,260 m, and then drops down to Ambaidiru (640 m). West of Serui on the south coast, another road was under construction towards Ambaidiru but stopped at an elevation of 146 m. From a base in Serui, KDB used a vehicle to survey birds along all of these roads during his six days on Yapen.

2017.—JD & KDB arrived in Serui by plane 13 October and departed on 20 October. From our base in Serui, we travelled by four-wheel-drive vehicle to survey sites along the trans-island road, the Ambaidiru road, and the north and south coastal roads. On three days we surveyed the Ambaidiru road from its crest at 1,260 m to its junction with the trans-island road at 655 m. We surveyed the trans-island road from its crest at 938 m to 760 m in the southern watershed on two days, and to 365 m in the northern watershed on two others. On seven days we surveyed the river crossing at 126 m on the trans-island road. On one day each we made observations on the north coast road east from its junction with the trans-island road, and the south coast road west from Serui to the airport.

Methods

Our methods were similar to those that we described for our work in the Fakfak and Kumawa Mts. (Diamond & Bishop 2015). Briefly, most of JD's observations in 1983 were on foot trails in the forest, while all of our observations in 2016–17 were on roads, of which all except the coastal roads are narrow and mostly lined and overhung by forest. We devoted much effort to recording vocalisations with Sony TCM 5000 EV tape recorders, playing back unidentified vocalisations in the field to attract and identify singers, and re-listening to recordings in camp each day because our directional microphones often captured calls that we had not noticed in the field. We stopped at fruiting and flowering trees where birds gathered. We began observations by 04.00 h to detect nocturnal birds. Elevations of all significant observations were measured using Thommen altimeters or a Garmin GPS. The only collecting consisted of three mist-nets operating for three days at 1,000–1,100 m near Ambaidiru in 1983. Of the 11 individuals captured, ten were weighed and released. The remaining bird (the type of Green-backed Robin *Pachycephalopsis hattamensis insularis*) was prepared as a specimen for the Museum Zoologicum Bogoriense, Bogor, Indonesia. A previous paper (Diamond 1985) described that subspecies and mentioned 12 other species records on Yapen. We also made observations in the Yapen lowlands during all three of our visits, but this paper reports only on upland species. Our nomenclature follows Beehler & Pratt (2016), with one exception suggested by further information (see *Sericornis beccarii* under Species accounts).

Results

This paper discusses a fraction of Yapen's avifauna: its upland species, defined as those species largely confined to sloping elevated terrain, and absent from the level-ground lowlands at or near sea level. The literature concerned with avian distributions on tropical mountains often refers to 'montane species', namely those largely confined to altitudes above some specified elevation, e.g., for New Guinea, 800 or 1,600 m (Stresemann 1923) or 1,700 m (Archbold & Rand 1935). That would be appropriate if there was a sharp break in distributions of many bird species at the specified elevation. In reality, elevational floors of New Guinea bird species are distributed continuously without concentration at any specific elevation (Diamond 1972b: 67–70). Consequently, a definition of species as montane if their elevational floor exceeds some specified value is completely arbitrary.

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We have instead found it useful to characterise species as absent in New Guinea's flat lowlands ('upland species') or else present there ('lowland species'). Of course, this definition also poses its own ambiguities and requires some arbitrary decisions, but those problems are much fewer than those in invoking an arbitrary elevational cut-off. The main ambiguities in New Guinea involve the following: species that breed at high elevation but descend post-breeding to the lowlands (e.g., Ornate Fruit Dove *Ptilinopus ornatus*); hill species of sloping terrain that descend to near sea level in such terrain but are absent from level-ground lowlands near sea level (e.g., Torrent Flycatcher *Monachella muelleriana*); borderline cases of species that occur mostly in sloping elevated terrain, but of which occasional individuals occur in the flat lowlands (how frequent must such 'occasional' encounters be to disqualify a taxon as an upland species?); borderline cases of species confined to mountains at most localities but with a few populations at sea level (e.g., Hooded Pitohui *Pitohui dichrous*); and 17 species confined to higher elevations in northern New Guinea but with sea level populations around southern New Guinea's Fly River mouth and / or on the Aru Islands (to be discussed in connection with Table 6). Diamond & Bishop (2015: 299–300) provided more examples of borderline cases.

Table 1 lists the 26 Yapen species that we regard as upland species under this definition. Characteristics tabulated for each species, and to be discussed in the text, are Yapen records, ability to disperse overwater, whether or not the Yapen population is regarded as an endemic subspecies, abundance and elevational floor on Yapen, and presence and abundance on the most nearly comparable outlying mountain ranges on the New Guinea mainland. Our concluding section of species accounts provides details.

Completeness of survey

How complete is that list of 26 upland species for Yapen likely to be? Knowledge of Yapen birds was obtained initially by six individuals or teams who visited Yapen between 1869 and 1897, evidently confined to the south coast and low elevations, and providing specimens but no field observations. Those specimens document ten upland species. Stein was the first collector to camp at higher elevation (950 m) in Yapen's interior. His specimens include four of the nine upland species recorded previously, plus six new records. However, Stein provided no field observations for Yapen birds, other than mentioning two conspicuous lowland species that he reported seeing on a brief second visit but did not collect (Rothschild *et al*. 1932: 216: Hooded Pitta *Pitta sordida* and Brown Oriole *Oriolus szalayi*). No previous or subsequent observer has recorded these two species on Yapen, so we suspect that Stein's comment refers to a different locality.

Our three visits recorded all but one (Meyer's Goshawk *Accipiter meyerianus*) of the 16 upland species previously collected on Yapen. We added seven new records. Advantages that we enjoyed over previous visitors included ascending the highest of Yapen's western peaks (1,340 m), familiarity with New Guinea bird vocalisations, extensive sound-recording with playback, and being able to devote most of our time to observing rather than collecting and preparing specimens.

Verhelst & Pottier (2020) added three more upland species in 2019, yielding a total of 26. Of this total, three are based on the observation or collection of a single individual by just one visitor or team (*Accipiter meyerianus*, Pygmy Eagle *Hieraaetus weiskei* and Yellow-legged Flyrobin *Kempiella griseoceps*). Two records (Dimorphic Jewel-babbler *Ptilorrhoa* cf. *geislerorum* and Black-eared Catbird *Ailuroedus melanotis*) are based on two observations of each species by Verhelst & Pottier (2020). Four (Chestnut-backed Jewel-babbler *Ptilorrhoa castanonota*, White-faced Robin *Tregellasia leucops*, White-rumped Robin *Peneothello bimaculata* and *Pachycephalopsis hattamensis*) were recorded on two visits, and two others

ISSN-2513-9894 (Online)

TABLE 1
Yapen's upland species.

Species	Records	Water-crosser?	No. of outliers	Endemic subspecies	Abundance	Floor (m)	VFAK	Outlier abundance
Wattled Brushturkey *Aepypodius arfakianus*	83, D, V	no	9	no/yes	2	?	VFK	1
Black-billed Cuckoo-Dove *Macropygia nigrirostris*	83, 17, S	yes	10	no/no	2	1,160, 0	VFAK	3
Pheasant Pigeon *Otidiphaps nobilis*	83, 17, D	yes	9	no/yes	1	580	VFAK	2
White-bibbed Fruit Dove *Ptilinopus rivoli*	83, 16, 17, S, Br, D, R, V	yes	10	no/yes	3	510	VFAK	3
Claret-breasted Fruit Dove *Ptilinopus viridis*	83, 17, S, Br, D, R	yes	8	no/yes	3	520	VFK	3
Papuan Mountain Pigeon *Gymnophaps albertisii*	83, S, D, G	yes	10	no/yes	1	450	VFAK	2
Mountain Swiftlet *Aerodramus hirundinaceus*	83, 17, S	yes	7	yes/yes	2	?	FAK	2
Pygmy Eagle *Hieraaetus weiskei*	16	yes	4	?/no	1	?	A	1
Meyer's Goshawk *Accipiter meyerianus*	M	yes	2	?/no	1	?	K	1
Black-eared Catbird *Ailuroedus melanotis*	V	no	9	?/yes	2	?	VFAK	2
Red Myzomela *Myzomela cruentata*	83, 16, 17, S, V	yes	8	no/yes	2	450	FAK	2
Mountain Meliphaga *Meliphaga orientalis*	83, 16, 17, V	no	8	?/yes	3	1,005	FAK	3
White-eared Meliphaga *Meliphaga montana*	83, 16, 17, S, V	no	9	yes/yes	3	795	VFAK	3
Tropical Scrubwren *Sericornis beccarii*	83, 16, 17, S, V	no	8	yes/yes	4	450	VFK	3
Dimorphic Jewel-babbler *Ptilorrhoa* cf. *geislerorum*	V	no	2	?/no	2	?	A	2.5
Chestnut-backed Jewel-babbler *Ptilorrhoa castanonota*	83, 17	no	9	?/yes	3	665	VFAK	2.5
Stout-billed Cuckooshrike *Coracina caeruleogrisea*	83, 17, M, R	no	10	no/no	2	855	VFAK	2
Papuan Cicadabird *Edolisoma incertum*	83, 17, Br, M, V	no	10	no/no	4	645	VFAK	3
Hooded Pitohui *Pitohui dichrous*	83, 17, S, V	no	10	no/no	4	450	VFAK	4
Green-backed Robin *Pachycephalopsis hattamensis*	83, 17	no	4	yes/yes	2	610?	V	3
Yellow-legged Flyrobin *Kempiella griseoceps*	V	no	5	?/no	1	?	VFAK	1
White-rumped Robin *Peneothello bimaculata*	83, 17	no	5	?/yes	1	900	VA	3
White-faced Robin *Tregellasia leucops*	83, V	no	9	?/yes	2	665	FAK	2.5
Magnificent Bird of Paradise *Cicinnurus magnificus*	83, 17, S, Be, D, G, M, R, V	no	10	no/yes	3	425	VFAK	4
Island Leaf Warbler *Seicercus poliocephalus*	83, 16, 17, V	yes	9	?/yes	4	675	FAK	4
Green-fronted White-eye *Zosterops minor*	83, 16, 17, S, D, M, V	no	10	no/yes	4	425	VFAK	3

Column 2. Records. Yapen records are coded as follows: 83, 16, 17 = our own observations in 1983, 2016 and 2017; S = Stein in 1931; 19th-century collections: Be = Beccari, Br = Bruijn, D = Doherty, G = Guillemard, M = Meyer, R = Rosenberg; V = Verhelst & Pottier in 2019.

Column 3. Water-crosser. Has the species demonstrated the ability to colonise overwater, as shown by its presence on oceanic islands near New Guinea but without a recent land bridge to the latter? See text for list of such islands.

Column 4. No. of outliers. Of the ten outlying mountain ranges of the New Guinea mainland, on how many does the species (or another allospecies of its superspecies in two cases) occur?

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Column 5. Endemic subspecies. The first no/yes entry asks whether the Yapen population has been diagnosed as an endemic subspecies. (? = no specimen has been analysed to date). The second no/yes entry asks if subspecies of the species are recognised in the New Guinea region; if 'yes' but the answer to the first entry is 'no,' then the Yapen population has failed to subspeciate despite that the species has subspeciated elsewhere in the New Guinea region.

Column 6. Abundance on Yapen, as estimated on a scale from 1 (least abundant species) to 4 (most abundant species).

Column 7. Elevational floor on Yapen, in metres. ? = too few records at known elevations to assess the floor of that species. Double entry (1,160, 0) for *Macropygia nigrirostris* indicates calling individuals and presumed breeding occur down to 1,160 m, but silent, presumably non-breeding birds recorded to sea level.

Column 8. VFAK? Presence on four mainland outliers most similar in elevation to Yapen. V = Van Rees (authors' unpubl. obs.). FK = Fakfak and Kumawa (Diamond & Bishop 2015). A = Adelbert (Gilliard & LeCroy 1967, Pratt 1983, Beehler & Pratt 2016; pers. obs.).

Column 9. Abundance averaged over those four mainland outliers, as estimated on a four-point scale.

(Wattled Brushturkey *Aepypodius arfakianus* and Pheasant Pigeon *Otidiphaps nobilis*) on three. The other 15 species were recorded on multiple occasions during four or more visits.

These facts suggest that some local or rare upland populations await discovery on Yapen. Our guess is that particular attention is warranted for the following 11 currently unrecorded species, because they occur on multiple mainland New Guinea outliers, and because Yapen lies within their elevational range, but they are inconspicuous, uncommon, and / or local, so they may have been overlooked to date: Dwarf Cassowary *Casuarius bennetti*, White-eared Bronze Cuckoo *Chalcites meyerii*, Wallace's Owlet-nightjar *Aegotheles wallacii*, Red-breasted Pygmy Parrot *Micropsitta bruijnii*, Barred Cuckooshrike *Coracina lineata*, Spotted Honeyeater *Xanthotis polygrammus*, Obscure Honeyeater *Caligavis obscura*, Greater Melampitta *Megalampitta gigantea*, *Monachella muelleriana*, Russet-tailed Thrush *Zoothera heinei* and Blue-faced Parrotfinch *Erythrura trichroa*.

Upland species number

We now compare the number of upland species on Yapen (S_{up}) with those on three other sets of islands or mountains: oceanic islands of the Papuan region and northern Melanesia; the other land-bridge islands of the Papuan region besides Yapen; and the ten outlying mountain ranges of the New Guinea mainland.

Oceanic islands.—We first compare S_{up} on Yapen with that on specific mountainous oceanic islands of the Papuan region and northern Melanesia. Karkar in the Papuan region is higher than Yapen (1,831 vs. 1,430 m) but has less than one-third as many upland species (eight vs. 26: Diamond & LeCroy 1979: 486). Goodenough and Fergusson in the Papuan region are higher than Yapen (2,536 and 1,864 m, respectively) but also possess considerably fewer upland species (*c*.16 and 15, respectively: Beehler & Pratt 2016). Northern Melanesia has ten islands similar to Yapen in elevation (1,040–1,768 m, mean 1,288 m), but those islands have less than one-quarter as many upland species as Yapen (on average six, range 1–15; Mayr & Diamond 2001: 59–60). Even the three highest northern Melanesian islands (Bougainville, Guadalcanal and New Britain), with elevations almost double Yapen's (2,591, 2,448 and 2,439 m, respectively), support fewer upland species than Yapen (18, 23 and 16, respectively).

In addition to these comparisons with individual oceanic islands, we can make a more specific calculation for Yapen itself. If the latter was an oceanic island with no recent land connection to New Guinea, its expected number of upland species could be calculated as follows. For oceanic islands 8–500 km from New Guinea, the number of resident lowland land and freshwater bird species S is described by the equation $S = 12.3\ A^{0.22}$, where A = area in square kilometres (equation 1 of Diamond 1973); and the number of upland species S_{up} is described by the formula 0.089 SL/1,000 where L = elevation in metres. For Yapen (A

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TABLE 2

Populations of upland species on West Papuan Islands. Like Yapen, these are land-bridge islands that were formerly part of mainland New Guinea, but being geographically distant from Yapen they constitute 'natural experiments', independent of Yapen, in colonisation and survival of upland species on land-bridge islands. Nevertheless, while just 15 of New Guinea's 193 upland species occur on the West Papuan Islands, ten of them also occur on Yapen. This illustrates that certain upland species are disproportionately successful, and others disproportionately unsuccessful, in colonising and persisting on mountainous land-bridge islands. The summit elevation of each island appears below the island's name at the head of its column.

Species	**Water-crosser?**	**No. of outliers**	**Misool 509 m**	**Salawati 781 m**	**Waigeo 974 m**	**Batanta 1,172 m**	**on Yapen? 1,430 m**	**Arafura**
Wattled Brushturkey *Aepypodius arfakianus*	no	9	✓	--	[√]	--	✓	--
Claret-breasted Fruit Dove *Ptilinopus viridis*	yes	8	--		lowlands	✓	✓	--
Pheasant Pigeon *Otidiphaps nobilis*	yes	9	--	--	✓	✓	✓	✓
White-eared Bronze Cuckoo *Chalcites meyerii*	no	10	--	--	--	✓	--	--
Wallace's Owlet-nightjar *Aegotheles wallacii*	no	2	--	--	✓	--	--	✓
Black-eared Catbird *Ailuroedus melanotis*	no	9	lowlands	--	--	--	✓	✓
Spotted Honeyeater *Xanthotis polygrammus*	no	9	lowlands	lowlands	✓	--	--	
Mountain Meliphaga *Meliphaga orientalis*	no	8	--	--	✓	--	✓	--
White-eared Meliphaga *Meliphaga montana*	no	9	--	--	--		✓	--
Tropical Scrubwren *Sericornis beccarii*	no	8	--	--	✓	--	✓	✓
Chestnut-backed Jewel-babbler *Ptilorrhoa castanonota*	no	9	--	--	--	✓	✓	--
Barred Cuckooshrike *Coracina lineata*	yes	8	--	--	lowlands	--	--	
Papuan Cicadabird *Edolisoma incertum*	no	10	--	--	✓	✓	✓	--
Magnificent Bird of Paradise *Cicinnurus magnificus*	no	10	--	✓	[√]	[√]	✓	--
Banded Yellow Robin *Gennaeodryas placens*	no	4	--	--	--	✓	--	--
Total species			**1**	**2**	**8**	**8**		

Column 2 (water-crosser?) and Column 3 (# outliers) as columns 3–4 in Table 1.

Check mark = present on that land-bridge island as an upland population, in our field experience on the relevant island.

'lowlands' = the species is an upland taxon on New Guinea, and usually also on Yapen, but its population on the land-bridge island occurs in the flat lowlands, in our field experience on the relevant island.

[√] = present as an insular allospecies of a superspecies present on mainland New Guinea. Sources: Mayr (1941), Beehler & Pratt (2016), and pers. obs.

Column 8. √ = present as an upland population on Yapen.

Column 9. √ = present as a relict lowland population on the two extant fragments of the large Arafura platform exposed in the Pleistocene, but then mostly inundated at the end of that era (eee Table 6 and text for discussion).

= 2,230 km^2, L = 1,430 m) those formulas yield an expected S_{up} value of nine species: far less than Yapen's actual S_{up} value of 26 species.

Thus, Yapen possesses more upland species than the most nearly comparable mountainous islands near New Guinea but with no recent land connections to the latter, and more than calculated for an oceanic island of Yapen's area and elevation. The explanation is clear: Yapen received upland species overland from New Guinea's Central Range and other outliers whenever it was connected to the New Guinea mainland, as well as overwater

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at other times, whereas the oceanic islands have always received species only overwater. That conclusion for upland species also applies to lowland taxa: Yapen and the other large Papuan land-bridge islands all possess more lowland species than do similar-sized oceanic islands near New Guinea (Diamond 1972a).

Land-bridge islands.—The Papuan land-bridge islands most similar to Yapen are Batanta, Waigeo, Salawati and Misool (elevations 1,070, 970, 686 and 565 m, respectively), which resemble Yapen in lying on New Guinea's continental shelf and in having formed part of Pleistocene New Guinea. (It is unknown whether today's very narrow Sagewin Strait between Salawati and Batanta, which was an important geological feature and biogeographic boundary in the past, existed during the late Pleistocene.) Those four islands support eight, eight, two and one upland species, respectively (Table 2), i.e. many fewer than Yapen, because all of those islands are lower-lying. The remaining large Papuan land-bridge island, Aru, is so low (241 m) that it is not known to harbour any upland population.

New Guinea mountain outliers.—Of New Guinea's ten outlying ranges (elevations 1,262–4,121 m), all are considerably lower than the Central Range (4,884 m), but six are rather higher (1,886–4,121 m) than Yapen. The four outliers most nearly comparable to Yapen in elevation are Van Rees (1,262 m), Fakfak (1,400 m, closest to Yapen's elevation of 1,430 m), Adelbert (1,675 m) and Kumawa (1,654 m). Their S_{up} values of 34, 65, 67 and 72 species, respectively (Diamond & Bishop 2015; unpubl. obs.) are much higher than Yapen's 26 species. When Yapen was part of the New Guinea mainland until around 10,000 years ago, it was just another outlier, with a higher species total presumably similar to that of those four comparable outliers, and probably most similar to that of Fakfak (65 species). After the inundation of the land bridges turned Yapen, Batanta, Waigeo, Salawati and Misool into islands, preventing overland immigration, their populations of both lowland and upland species declined due to extinctions no longer being balanced by the overland immigration rates prevailing when they formed part of the mainland.

In short, Yapen has many fewer upland species (and also fewer lowland species: Diamond 1972a) than a piece of the New Guinea mainland of similar elevation and area. But, conversely, it has many more upland species (and also more lowland species: Diamond 1972a) than an oceanic island of similar elevation and area. That is, Yapen and the other large land-bridge islands are 'supersaturated' in species: they started out with the species richness of pieces of the New Guinea mainland when they were just part of that mainland during the Pleistocene; since the land bridges were severed around 10,000 years ago, they have been losing species by excess extinctions; but they still possess more species than comparable oceanic islands, although they already have fewer species than comparable areas of the New Guinea mainland (Diamond 1972a).

Upland species identities

Species differences in occurrence frequency.—Having compared Yapen's number of upland species with numbers on the most comparable mainland outliers, we now compare the identities of the upland species. The 34, 65, 67 and 72 upland species of Van Rees, Fakfak, Adelbert and Kumawa include most of Yapen's 26 upland species: 18, 21, 22 and 22 species, respectively. In turn, Yapen's upland species include most of those of the four lower land-bridge islands: six of Waigeo's eight, six of Batanta's eight, both of Salawati's two, and Misool's one. But the total of 193 upland species for New Guinea greatly exceeds any of the species totals shared between Yapen and the four most comparable mainland outliers, or between Yapen and the other four large land-bridge islands with upland species. Table 2 shows that the 19 upland populations on those other four land-bridge islands belong to only 15 different species, of which ten have upland populations on Yapen. This suggests that,

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TABLE 3

Upland species distributions on New Guinea's outliers. For each of New Guinea's 193 upland species, we tabulated how many of New Guinea's ten outliers the species occupies. That number (column 1) ranges from 0 (no outlier occupied) to 10 (all ten occupied). Column 2: the number of New Guinea upland species occupying that number of outliers. Column 3: the product of columns 1–2: i.e., the number of outlier populations attributable to species occupying that number of outliers. Column 4: the number of Yapen species attributable to species occupying that number of outliers. (For example, there are 20 New Guinea upland species which each occupy eight outliers; hence those 20 species account for 20 × 8 = 160 outlier populations; and four Yapen upland species belong to that group of 20.) See text for discussion. Sources: see Table 1 legend for four outliers; Beehler *et al*. (2012) for Foja; and Hartert (1930), Mayr (1931, 1941), Gyldenstolpe (1955), Freeman *et al*. (2013), Beehler & Pratt (2016) and LeCroy & Diamond (2017) for the five others.

No. of outliers occupied	**No. of species occupying that number of outliers**	**No. of outlier populations**	**No. of Yapen species**
0	35	0	0
1	29	29	0
2	19	38	1
3	17	51	2
4	14	56	1
5	13	65	1
6	10	60	0
7	10	70	2
8	20	160	4
9	17	153	7
10	9	90	8
Total	**193 species**	**772 populations**	**26 species**

of New Guinea's 193 upland species, only a small subset occurs repeatedly on mainland outliers, and an even smaller subset do likewise on the land-bridge islands.

Table 3 explores this suggestion systematically by tabulating, for each of New Guinea's 193 upland species, on how many of the ten mainland outliers that species occurs. It can be seen that 35 species occur on none of the outliers, and almost half of the 193 (83 species = 39%) are on just 0–2 outliers, but nine species occur on every outlier and 46 species on 8–10 of the ten outliers. Those 46 most widely distributed species represent only 24% of New Guinea's upland species but account for 52% of outlier populations. Evidently, some species are disproportionately successful colonists, others are disproportionately unsuccessful, and fewer are intermediate. Table 3 also demonstrates that 24% of the upland avifauna that accounts for half of the outlier upland populations also accounts for most—19 of 26, or 73%—of Yapen's upland populations.

That is, upland species successful at colonising mainland outliers have also been successful at colonising and persisting on Yapen. The explanation is presumably that Yapen *was* a mainland outlier until its land bridge to the New Guinea mainland was severed *c*.10,000 years ago. Thus part of the explanation for the composition of Yapen's upland avifauna consists of the same factors (whatever they may be) explaining the compositions of the upland avifaunas of the ten outliers. The other part of the explanation for the composition of Yapen's upland avifauna consists of factors explaining why Yapen has fewer upland species than comparable mainland outliers, i.e. why some of Yapen's upland populations that it inherited >10,000 years ago have subsequently become extinct, while others have not. We explore both sets of factors in the next sections.

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Effects of elevation.—New Guinea's Central Range reaches its highest point at 4,884 m and large areas are above 2,000 m. As a result, the Central Range has a rich upland avifauna including many species whose elevational floors exceed 2,000 m, ranging up to a highest floor of 3,800 m (Snow Mountain Robin *Petroica archboldi*). In contrast, the highest outliers are 4,121 m (Huon) and 2,954 m (Vogelkop), and only three others just exceed 2,000 m (2,075–2,218 m). Nor is it the case that an outlier whose summit is at 2,218 m (Foja) can support populations of Central Range species with floors exceeding 2,000 m, because the area at high elevation of even the tallest outliers is small. The highest floors of any species population on an outlier are between 270 and 940 m below its summit, e.g. 500 m below the summit for Foja (Beehler *et al*. 2012), 265 m below the summit for Kumawa (Diamond & Bishop 2015) and almost 1,000 m below it for the Vogelkop.

Consequently, elevation explains more than half of the cases of the 35 New Guinea upland species present on no outlier. Of the 35, 20 are high-elevation species: 16 have floors ≥ 2,000 m, and six of those 16 have floors above 3,000 m. (The other 15 absentees that are not high-elevation species are absent from outliers for idiosyncratic reasons, such as there being no outlier within their geographic range.) Similarly, of the 29 species present on just one outlier, 28 are high-elevation species whose sole outlier population is on one of the two highest, Huon (4,121 m) or Vogelkop (2,954 m). It was thus inevitable that Yapen supports no population of these 64 species present on just one or no mainland outlier. Yapen's summit is only 1,430 m; the highest well-attested elevational floors on Yapen are 1,160 m for the breeding population of Black-billed Cuckoo-Dove *Macropygia nigrirostris*, 1,005 m for Mountain Meliphaga *Meliphaga orientalis* and 855 m for Stout-billed Cuckooshrike *Coracina caeruleogrisea*. Hence elevation explains a large fraction of absences of Central Range upland species on the mainland outliers and on Yapen.

Water-crossing ability.—Many tropical forest species are reluctant to cross clearings or fly above the canopy. Even among those species that do cross clearings or fly above the canopy over land, many have never been observed flying over water and have never been recorded on any island lacking a recent land connection to the source island. In New Guinea, for example, Papuan Spinetailed Swift *Mearnsia novaeguineae* feeds entirely by long flights in the open, and Dusky Lory *Pseudeos fuscata*, Black Lory *Chalcopsitta* [*atra*] and Blue-collared Parrot *Geoffroyus simplex* are regularly seen flying high and for long distances between roosts and feeding grounds, but none of these has ever been recorded from any New Guinea island lacking a recent land bridge. These and 300 other New Guinea species possess a behavioural refusal to cross water gaps, although their flight capabilities would easily permit it, and some have close relatives that do cross such gaps (Diamond 1972a).

We define water-crossing species as those of the New Guinea mainland recorded from any 'oceanic' island lacking a recent land connection. The oceanic islands with the most such records are Karkar, Biak, the D'Entrecasteaux Islands, and the Bismarck and Solomon Islands. By that definition, of New Guinea's 193 upland species, only 29 are water-crossers; the other 164 are strictly confined to New Guinea and its large land-bridge islands.

Table 4 tabulates water-crossers and non-water crossers among the upland species on Yapen and the four most comparable mainland outliers. It is apparent that Yapen has a considerably higher percentage of water-crossers than any of the mainland outliers (38% vs. 18–25%), mainly because Yapen has considerably fewer non-water-crossers (16 vs. 28–55 species), although a similar number of water-crossers (ten vs. 6–17 species). (Of course water-crossing populations of the mainland outliers reached there from the Central Range overland, not overwater; ability to disperse overwater does not preclude ability to disperse overland.) The straightforward explanation is that, once Yapen's land bridge to New Guinea was severed at the end of the Pleistocene making Yapen an island, populations now isolated

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TABLE 4

Water-crossing ability of upland species: total numbers, number of water-crossing species, and number of non-water-crossing species. Species are considered water-crossers if recorded from any 'oceanic' island lacking a recent land bridge to New Guinea (most records on Karkar, Biak, D'Entrecasteaux Islands, and the Bismarck and Solomon Islands). Non-water-crossers are species unrecorded on any oceanic island, but in many cases recorded on Yapen and other land-bridge islands reachable overland from New Guinea during the Pleistocene. The four mainland outlying ranges tabulated (VFAK) are those also tabulated in Table 1 due to their similar elevation to Yapen. Note: Yapen's number of water-crossing upland species is similar to comparable outliers, but Yapen has only one-third of the non-water-crossing species as comparable outliers (because post-Pleistocene population extinctions after Yapen became an island could not be reversed by overwater recolonisation). See text for discussion.

Mountain	Total upland species	Water-crossing species	Non-water-crossing species	% water-crossers
V = Van Rees	34	6	28	18%
F = Fakfak	65	15	50	23%
A = Adelbert	67	17	50	25%
K = Kumawa	72	17	55	24%
average, VFAK	58	14	46	23%
Yapen	26	10	16	38%

thereon during the Holocene began going extinct. Those extinctions could be reversed by overwater colonisation by water-crossing taxa, but not for non-water-crossing species.

Therefore, two main reasons explain why Yapen possesses fewer upland species than the ten mainland outliers, and many fewer upland species than the Central Range: lack of habitat for New Guinea's high-elevation upland species (Yapen is significantly lower than six of the ten outliers, and much lower than the Central Range); and post-Pleistocene extinctions of non-water-crossing populations incapable of reversal by recolonisation overwater. Below we explore further those inferred post-Pleistocene extinctions.

Inferred extinctions.—The comparisons in the section Upland species number, such as the large deficit of upland species on Yapen vs. the Fakfak mainland outlier most similar to the former in elevation (26 vs. 65 species, respectively), imply that many upland populations have become extinct since the severing of Yapen's Pleistocene land bridge to New Guinea. But that comparison alone does not answer the question: *which* upland populations were present on Yapen at the time of the Pleistocene land bridge, and have subsequently become extinct?

In the absence of proof from fossils, a reasonable guess is: species that are present on several of the most similar mainland outliers (Van Rees, Fakfak, Adelbert, Kumawa), and whose elevational floors are within the range for populations still present on Yapen, but are absent on the island today. Table 5 lists the 23 such species. On average, they occur on three of the four comparable outliers; all have floors on Van Rees, Fakfak and Kumawa below Yapen's highest floor (1,160 m), all but one have floors on those outliers below 915 m, and most are below 800 m. (However, three of the 23 have floors above 1,160 m on Adelbert, where floors average slightly higher.) Naturally, we do not claim that all 23 of the absent species did become extinct on Yapen: some of them might by chance have initially been absent, and the four outliers are not perfect matches for Yapen, as we shall discuss in Mechanisms for colonising Yapen. We can only reason that those species are particularly likely to have been among the dozens that did go extinct there.

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TABLE 5

Upland species whose populations may have disappeared on Yapen. Column 1: the 23 upland species that seem especially likely to have been formerly present, but have now disappeared, based on two criteria: presence on two or more of the four mainland outliers closest to Yapen in elevation; and elevational floors on those outliers well below 1,160 m (the highest floor of any Yapen population) and mostly below 800 m (most Yapen floors are below 800 m). On average, the 23 species are present on three of the four outliers; 17 of the 23 occur on either three or all four outliers. Column 2: water-crosser? Column 3: number of mainland outliers occupied (as columns 3–4 in Table 1). Columns 4–7: elevational floors on four outliers (from Diamond & Bishop 2015 for Fakfak and Kumawa, and our unpubl. obs. for Van Rees and Adelbert). Abbreviations F, V, K, A as Table 4. Column 8: average abundance on Fakfak and Kumawa, as assessed by Diamond & Bishop (2015) on a scale from 1 (least common) to 4 (most common). For the four species present only on Van Rees and Adelbert, where we did not estimate abundance, we use instead JD's estimates for Foja (in Beehler *et al*. 2012). See text for discussion.

Species	Water-crosser?	No. of outliers	Floor (m)				Outlier abundance
			V	F	K	A	
Dwarf Cassowary *Casuarius bennetti*	no	7	549	?	?	730	2
White-eared Bronze Cuckoo *Chalcites meyerii*	no	10	549	--	113	820	2.5
New Guinea Vulturine Parrot *Psittrichas fulgidus*	no	7	366	--	--	820	1.5
Red-fronted Lorikeet *Charmosyna rubronotata*	yes	3	915	?	?	730	1.8
Blue-collared Parrot *Geoffroyus simplex*	no	8	366	617	553	820	2.5
Red-breasted Pygmy Parrot *Micropsitta bruijnii*	yes	9	--	774	704	1,220	2.3
Spotted Honeyeater *Xanthotis polygrammus*	no	9	823	635	--	1,000	1
Brown-breasted Gerygone *Gerygone ruficollis*	no	5	--	787	742	1,575	2.8
Mountain Peltops *Peltops montanus*	no	9	518	684	604	700	2
Barred Cuckooshrike *Coracina lineata*	yes	8	854	--	728	975	1
Black-bellied Cicadabird *Edolisoma montanum*	no	9	--	863	786	1,100	2.5
Piping Bellbird *Ornorectes cristatus*	no	8	580	657	483	--	2.5
Sclater's Whistler *Pachycephala soror*	yes	5	--	690	375	1,525	3
Rusty Whistler *Pachycephala hyperythra*	no	8	580	690	671	850	1
Drongo Fantail *Chaetorhynchus papuensis*	no	9	610	690	622	567	3
Trumpet Manucode *Phonygammus keraudrenii*	yes	8	143	399	128	930	4
Greater Melampitta *Megalampitta gigantea*	no	4	--	835	680	--	2.5
Fantailed Monarch *Symposiachrus axillaris*	yes	9	915	774	652	850	2.3
Black-winged Monarch *Monarcha frater*	no	8	--	689	411	750	2.8
Torrent Flycatcher *Monachella muelleriana*	yes	5	518	--	--	567	1
Papuan Scrub Robin *Drymodes beccarii*	no	7	610	--	--	995	2
Banded Yellow Robin *Gennaeodryas placens*	no	4	--	457	104	1,000	2.7
Blue-faced Parrotfinch *Erythrura trichroa*	yes	8	--	546	1,025	820	3.5

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What distinguishes the 23 populations likely to have become extinct on Yapen from the populations that have persisted there? For species unable to cross water, there is the expected effect of population abundance on extinction probability, with abundance estimated on mainland outliers and tabulated in Tables 1 and 5. Expressing abundance on a four-point scale from 1 (the rarest) to 4 (most abundant species), abundance ± S.D. averages 2.65 ± 0.80 (n = 16) for species present on Yapen, vs. 2.22 ± 0.60 (n = 15) for those absent on Yapen. That difference has a probability of 0.058 by a one-tailed t-test, close to the conventional level of $p = 0.050$ for concluding statistical significance. (A one-tailed t-test is more appropriate than a two-tailed test, because the hypothesis is not that species present or absent merely differ in abundance in either direction, but that species present are more abundant.) However, for water-crossing species, there is no effect of abundance on inferred survival: 2.38 ± 0.91 (n = 10) for species present on Yapen, vs. 2.36 ± 1.03 (8) for those absent on Yapen.

The straightforward interpretation is as follows. Populations of non-water-crossing species have been isolated on Yapen since the land bridge was severed. More abundant species have been more successful at surviving, in agreement with the discovery that population size is the strongest predictor of extinctions among isolated populations (MacArthur & Wilson 1967). There is no effect of abundance for water-crossing species, because their populations on Yapen have not been isolated since the land bridge was severed; many population extinctions could have been reversed by post-Pleistocene overwater colonisation; and an increased likelihood of less abundant populations to go extinct was perhaps offset by higher dispersal rates expected for less abundant species.

Those inferred post-Pleistocene extinctions of non-water-crossing species on Yapen could explain what we consider to be the most puzzling feature of the Yapen upland avifauna. Four of Yapen's 16 non-water-crossing populations are species widespread on mainland outliers and moderately or very common there, of which three are vocal and easily detected: *Ailuroedus melanotis*, *Tregellasia leucops*, *Pachycephalopsis hattamensis* and *Peneothello bimaculata*. But all four are rare and / or very local on Yapen, having been found on just one or two visits. Human hunting could not explain their rarity; all are small and not colourful, and none is a beautiful singer or targeted by hunters. We wonder if the Yapen populations of these four species that are common on the New Guinea mainland are on the verge of disappearing on Yapen, as we infer so many other insular populations have already done since the end of the Pleistocene. Historical demographic inferences from population genetic studies may provide interesting avenues for addressing population declines in these non-water-crossing species, as well as recent exchanges of genes and individuals in the water-crossers (see, e.g., Pool *et al*. 2010).

Mechanisms for colonising Yapen

If many individuals of New Guinea upland species were fitted with satellite-transmitters, we could observe the routes via which colonists reached the outliers from the Central Range or from other outliers. In the absence of such data, we can suggest six colonisation paths and histories using indirect evidence.

1. *Overwater colonisation*.—Of Yapen's 26 upland species, ten (see Table 1) are inferred to be capable of having arrived overwater when Yapen was (or, as it is today) an island—because the ten occur on other islands without recent connection to New Guinea. (Of course, the fact that they *could* have arrived overwater does not mean that they did so; they could have arrived overland during the Pleistocene, as did Yapen's 16 non-water-crossing species.) Among the ten species, it is highly probable that *Hieraaetus weiskei* and *Accipiter meyerianus* did arrive recently overwater, because they are rare hawks with low population

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densities, and only one individual of each has been observed on Yapen, making it unlikely that they represent populations large enough to have survived on Yapen for 10,000 years of isolation.

Among Yapen's ten water-crossers, four regularly fly high above the canopy: both just-mentioned raptors, Papuan Mountain Pigeon *Gymnophaps albertisii* and Mountain Swiftlet *Aerodramus hirundinaceus*. Three other species often fly through the canopy: White-bibbed Fruit Dove *Ptilinopus rivoli*, Claret-breasted Fruit Dove *P. viridis* and *Macropygia nigrirostris*. Red Myzomela *Myzomela cruentata* makes frequent movements in search of flowering trees. The remaining two water-crossers, the terrestrial pigeon *Otidiphaps nobilis* and the arboreal Island Leaf Warbler *Seicercus poliocephalus*, appear to be territorial and have never been observed flying above the canopy. These two species may colonise only or mainly during juvenile dispersal.

2. *Regular post-breeding descent to the lowlands*.—Two of Yapen's upland species, the pigeons *Macropygia nigrirostris* and *Gymnophaps albertisii*, are among the species that breed in New Guinea at high elevation but descend to the lowlands at other times. Such behaviour is also suggested for the Yapen population of *Macropygia nigrirostris* given that we heard it calling only above 1,160 m, but we saw silent individuals in the lowlands. This would facilitate dispersal by these two pigeons overland between the Central Range and outliers, including Yapen when it was connected to the mainland. Alternatively, both species could have reached Yapen overwater, because both occur on oceanic islands that could only have been reached overwater (Goodenough and New Britain, plus *M. nigrirostris* on Karkar).

3. *Occasional lowland stragglers or populations*.—Several other New Guinea species occur as occasional immature individuals below the species' usual elevational range, perhaps during juvenile dispersal (Diamond 1972b: 30–31). This behaviour operates to an extreme degree in some bird of paradise and bowerbird species, for which females and immatures regularly occur as much as 1,000 m below the elevation of displaying adult males (Stein 1936, Pruett-Jones & Pruett-Jones 1986). We have observed this phenomenon in New Guinea for two Yapen upland species, Magnificent Bird of Paradise *Cicinnurus magnificus* and Papuan Cicadabird *Edolisoma incertum* (Diamond 1972b: 335). In most parts of New Guinea *Pitohui dichrous* occurs above an elevational floor of at least 600 m, often as high as 1,100 m, but has some local lowland populations. All of these phenomena of occasional lowland presences would facilitate dispersal through the lowlands to mountains by species that are predominantly upland species.

4. *Dispersal via hill bridges vs.* 5. *Dispersal via flat lowlands*.—Most of the New Guinea outliers are connected to each other and / or to the Central Range by 'bridges' of low hills, either as a continuous chain or punctuated by very narrow lowland corridors. This permits dispersal of upland species entirely or mostly within hilly terrain.

The striking exceptions among the outliers are Fakfak and Kumawa, which are entirely separated from each other, from other outliers, and from the Central Range by a broad expanse of 70–100 km of flat lowlands close to sea level, without any hills. For some New Guinea upland species, level-ground lowlands apparently constitute a strong barrier. Pesquet's Parrot *Psittrichas fulgidus* occurs in hilly terrain up to 1,500 m and down to the base of the hills, but not in flat lowlands distant from the hills. It is so noisy and conspicuous in flight above the canopy that we can be confident that is absent from expanses of flat lowlands. Three other species—Salvadori's Teal *Salvadorina waigiuensis*, *Monachella muelleriana* and Torrentlark *Grallina bruijnii*—occur throughout along mountain rivers but do not follow them far into the flat lowlands.

All four of these species are absent from both Fakfak and Kumawa. This suggests that their colonisation of outliers depends on hill bridges, and not only do they not occur in

ISSN-2513-9894 (Online)

level-ground lowlands but they do not even disperse through these regions. Eleven other New Guinea upland species (listed in Diamond & Bishop 2015: 302, Table 2) are also absent from Fakfak and Kumawa, although they occupy 2–7 (on average, four) of the other eight outliers. None of those 11 other species has been reported from flat lowlands.

At the time that Yapen formed part of the New Guinea mainland, it, too, was separated from the nearest mountain (Van Rees) by 50 km of flat lowlands. Of the 15 species absent from Fakfak and Kumawa, 13—all of them except *Peneothello bimaculata* and *Pachycephalopsis hattamensis*—are also absent on Yapen. This suggests that, while the absence of those two species from Fakfak and Kumawa is unrelated to surrounding flat lowland terrain, many or most of the other 13 species really do depend on hill bridges for their dispersal.

6. *Pleistocene lowland relicts*.—During cold Pleistocene epochs, vegetation and climate zones on tropical mountains worldwide were depressed to elevations lower than currently. In New Guinea that lowering is supported by evidence such as glacial landforms being much more extensive and at much lower elevations than their current extent only at highest elevations. During those cold periods, some New Guinea upland species currently absent from the lowlands would have found suitable climate conditions in the lowlands. But those cold periods were also times of lower sea levels, which exposed as dry land an enormous platform connecting southern New Guinea to northern Australia, but now inundated as the shallow Arafura Sea (Fig. 1). As climate became warmer and sea level rose again at the end of the Pleistocene, most of the Arafura platform was drowned again, the Pleistocene lowland populations mostly disappeared, and their species again retreated upslope in New Guinea and became upland taxa.

But three legacies remained of the otherwise vanished lowland populations of upland species (Table 6), namely three sets of relict lowland populations of otherwise upland New Guinea birds, on the still-exposed parts of the platform furthest from the equator (hence in lowland areas climatically most similar to low elevations of New Guinea mountains). Those relicts are: 13 populations of upland species that the first and second Archbold Expeditions discovered at sea level on lowland New Guinea's southernmost bulge including the lower Fly River (Mayr & Rand 1937, Rand 1942); 11 populations on the Aru Islands, a fragment of the former platform surrounded by the Arafura Sea; and six of those species at the tip of Australia's Cape York Peninsula, even further from the equator (Fig. 1). Because the Aru Islands and Fly River bulge share lowland populations of seven upland species, but each has additional upland species not shared with the other, there is a total of 17 upland species with relict lowland populations still present on the Aru Islands and / or the Fly River bulge. Of the 17 species, seven have upland populations on Yapen, and six are represented on the Western Papuan Islands (Table 2).

We interpret these relict populations as evidence for one more mechanism whereby upland species colonised Yapen (and the Western Papuan Islands). Today, upland species are disjunctly distributed over New Guinea's outliers, the Central Range, and Yapen. But during cool eras in the Pleistocene, upland species shifted downslope, such that species with the lowest floors could have shifted into the lowlands and achieved continuous distributions. As climate warmed during the Holocene, these species shifted uphill again, abandoned the lowlands except relict populations in lowland areas furthest from the equator, and again became upland species with discontinuous distributions. Supporting this interpretation, Yapen's five upland species with relict lowland populations, and whose Yapen elevational ranges are best evidenced, have low elevational floors: on average, 600 m. Therefore it is plausible that they would have been species especially likely to shift downslope into the lowlands during the Pleistocene.

ISSN-2513-9894 (Online)

TABLE 6

Relict lowland populations of New Guinea upland species on the Arafura platform. The shallow Arafura Sea, which presently separates Australia from New Guinea, was exposed as a large lowland platform at Pleistocene times of low sea level. The Aru Islands, south New Guinea's Fly River bulge, and the north tip of Australia's Cape York Peninsula survive as fragments of the former platform. Today, one, two or all three of those fragments support lowland populations of 17 species that elsewhere in New Guinea are upland birds, and that are probably relicts of Pleistocene populations formerly widespread on that lowland platform. Seven of those species now have upland populations on Yapen. See text for discussion.

Species	**Fly River bulge**	**Aru Islands**	**Cape York tip**	**Yapen**
Pheasant Pigeon *Otidiphaps nobilis*	--	✓	--	✓
Wallace's Owlet-nightjar *Aegotheles wallacii*	--	✓	--	--
Black-eared Catbird *Ailuroedus melanotis*	✓	✓	✓	✓
Flame Bowerbird *Sericulus ardens*	✓	--	--	--
Spotted Honeyeater *Xanthotis polygrammus*	✓	--	--	--
Tropical Scrubwren *Sericornis beccarii*	✓	✓	✓	✓
Painted Quail-thrush *Cinclosoma ajax*	✓	--	--	--
Stout-billed Cuckooshrike *Coracina caeruleogrisea*	✓	✓	--	✓
Barred Cuckooshrike *Coracina lineata*	--	✓	--	--
Piping Bellbird *Ornorectes cristatus*	✓	--	--	--
Black-headed Whistler *Pachycephala monacha*	--	✓	--	--
Hooded Pitohui *Pitohui dichrous*	✓	--	--	✓
Trumpet Manucode *Phonygammus keraudrenii*	✓	✓	✓	--
Yellow-legged Flyrobin *Kempiella griseoceps*	✓	✓	✓	✓
Papuan Scrub Robin *Drymodes beccarii*	✓	✓	✓	--
White-faced Robin *Tregellasia leucops*	✓	--	✓	✓
New Guinea White-eye *Zosterops novaeguineae*	✓	✓	--	--

Future studies

Many questions concerning Yapen's avifauna remain unanswered. We conclude by calling attention to six of them:

1. What further upland populations remain to be discovered on Yapen? Some surely await discovery, because five of the 26 known upland populations have been observed by just one visitor. On p. 431 we suggested 11 'missing' species especially deserving of searches.

2. Endemic subspecies are recognised for some nine of Yapen's lowland populations, and for four of its upland populations (Rothschild *et al*. 1932, Mayr 1941, Rand & Gilliard 1967, Beehler & Pratt 2016). As expected, subspeciation has been reported for proportionately more of Yapen's upland populations than its lowland populations (19% vs. 7% respectively), although two of the three most distinctive races are *Paradisaea minor jobiensis* and *Pitohui kirhocephalus jobiensis* in the lowlands. Recently discovered Yapen upland populations not yet collected or identified subspecifically are *Meliphaga orientalis* (distinctive in the field: p. 444), *Ptilorrhoa castanonota*, *P.* cf. *geislerorum*, *Seicercus poliocephalus*, *Tregellasia leucops*, *Peneothello bimaculata* and *Ailuroedus melanotis*.

3. Bird fossils are unknown for Yapen, and for almost all of New Guinea. Fossils could provide direct evidence of the former existence of Pleistocene populations that we infer

ISSN-2513-9894 (Online)

existed but have vanished. Fossils could also provide evidence for when species arrived or disappeared.

4. Molecular phylogenetic and population genetic studies (e.g., Pool *et al*. 2010, Pedersen *et al*. 2018, Garg *et al*. 2020) could assess sources and relationships of Yapen's upland populations. The nearest upland sources are Van Rees, Wandammen, Vogelkop and the Central Range.

5. Molecular population genetic studies, as well as field observations, radio-tracking and banding, could provide tests of the dispersal mechanisms that we have postulated.

6. Yapen's lowland avifauna poses many of the same questions as its upland avifauna, but awaits a modern re-analysis to update that by Rothschild *et al*. (1932). The lowland avifauna comprises five times more species than in the uplands and offers rich material for analysis. Why does Yapen today harbour just 40% of New Guinea's lowland species? Yapen's lowlands were presumably much more species-rich when Yapen was still part of the mainland until 10,000 years ago: how can we explain why certain species of the New Guinea lowlands have been more successful than others at surviving on Yapen, and on five other large land-bridge islands?

Species accounts: Yapen's upland bird species

[**DWARF CASSOWARY** *Casuarius bennetti*
The sole cassowary species well evidenced on Yapen is the large lowland Northern Cassowary *C. unappendiculatus*, collected by Beccari and by Laglaize. But Rothschild (1914) described a new subspecies of the small montane species *C. bennetti*, from an individual brought alive to England by Walter Goodfellow from Yapen, presumably a captive, possibly bought as a chick. We saw no cassowaries of any species nor their droppings on our three visits, although Ambaidiru residents described cassowaries using the Yawa language name of 'apara'. Informants were equivocal as to whether they were familiar only with a large cassowary or also with a small one. New Guineans transport captive cassowaries widely, which is presumably how they became established on New Britain and Seram outside the Papuan region. Until *C. bennetti* is observed or collected in the wild on Yapen, its presence should be considered unproven.]

WATTLED BRUSHTURKEY *Aepypodius arfakianus*
JD observed one individual and saw a nest mound near the summit of Mt. Aror. The only specimen for Yapen is one that Doherty purchased on the coast, presumably brought from the mountains. Ambaidiru residents described this megapode and its mounds as 'ajinda', distinct from the other two Yapen megapodes, Red-legged Brushturkey *Talegalla jobiensis* = 'wayan' and New Guinea Scrubfowl *Megapodius decollatus* = 'mangkio'. Verhelst & Pottier (2020) obtained several photos from camera traps at different locations, suggesting that the species is common.

BLACK-BILLED CUCKOO-DOVE *Macropygia nigrirostris*
On Yapen, as elsewhere in the New Guinea region, the species called frequently and presumably was breeding only at high elevations (1,160 m), but was encountered silently (presumably non-breeding) at low elevations (700 m to sea level).

WHITE-BIBBED FRUIT DOVE *Ptilinopus rivoli*
By far the commonest *Ptilinopus* in the mountains of Yapen, from the summit to 510 m. There are two vocalisations, both similar to those of Mountain Fruit Dove *P. bellus* of mainland

ISSN-2513-9894 (Online)

New Guinea (if that is considered a different species): a series of slightly upslurred *hoo* notes starting very slowly and at a constant pitch, then accelerating, and descending in pitch; and a single *hoo* initially slightly upslurred, then markedly downslurred, repeated *ad nauseam* every five seconds. Beehler & Pratt (2016: 80) suspected that identification of the Yapen population as the small-island allospecies *P. rivoli* might be mistakenly based on specimens collected on nearby small islands, and that the Yapen population might represent the New Guinea mainland allospecies *P. bellus*. While that suspicion was reasonable, the relevant specimens attributable with certainty to Yapen are two collected by Stein at his 450-m camp on two different dates, and are both *P. rivoli miquelii*, not *P. bellus* (Rothschild *et al*. 1932: 242). Yawa name: 'irán'.

CLARET-BREASTED FRUIT DOVE *Ptilinopus viridis*
From 1,100 m down regularly to 520 m, occasionally in the lowlands, and often heard but infrequently seen. The two distinct vocalisations on Yapen are similar to those in all of the outlying ranges on New Guinea's north coast from the Kumawa Mts. east to the North Coastal Range of Papua New Guinea. One vocalisation consists of a detached first note, followed by *c*.6 pairs of notes, the first note of each pair on a lower pitch, the second accented, higher pitched and upslurred. The other vocalisation is a repeated three-note phrase, the first short, the second a higher pitched downslur and the third note a lower pitched downslur. On Yapen but not elsewhere, that second vocalisation is sometimes reduced to a repeated two-note phrase. Yawa name: 'omande'.

PAPUAN MOUNTAIN PIGEON *Gymnophaps albertisii*
Observed only in 1983: a flock of 30 seen daily at 905–1,100 m, feeding on drupes of the tree *Haplolobus floribundus* (Burseraceae). Yawa name: 'mansauman'.

PHEASANT PIGEON *Otidiphaps nobilis*
Heard just once in 1983 at 580 m, and once in 2017 at 650 m, but familiar to Ambaidiru residents by the Yawa name: 'wanaum'. Previously recorded only by Doherty.

MOUNTAIN SWIFTLET *Aerodramus hirundinaceus*
Brown swiftlets were seen in 1983 in large numbers at and above Ambaidiru (640 m), and in 2017 uncommonly from the lowlands to 1,195 m. We assume that swiftlets at high elevation were predominantly *A. hirundinaceus* (collected by Stein), and that those at low elevation were Uniform Swiftlet *A. vanikorensis*. Yawa name: 'kamantiováni' (for all species of swiftlets).

PYGMY EAGLE *Hieraaetus weiskei*
The sole record is of one observed soaring at 600 m by KDB in 2016.

MEYER'S GOSHAWK *Accipiter meyerianus*
The only record is a specimen acquired from an unknown location by A. B. Meyer.

BLACK-EARED CATBIRD *Ailuroedus melanotis*
Observed and photographed at 1,080 and 1,300 m (Verhelst & Pottier 2020).

RED MYZOMELA *Myzomela cruentata*
In 1983 JD observed both sexes regularly in white-flowered *Eugenia* trees at 1,005–1,100 m, but nowhere else. In 2016 KDB observed one male in a flowering tree at 1,100 m. Our only

ISSN-2513-9894 (Online)

sighting in 2017 was of a single male at 1,220 m. Verhelst and Pottier (2020) observed one at 950 m.

MOUNTAIN MELIPHAGA *Meliphaga orientalis*
First record for Yapen; the only other insular population is on Waigeo. Similar to Mimic Meliphaga *M. analoga* of Yapen's lower elevations, but distinguished with effort and practice both visually and by voice. Both species are large, yellow-eared, with long slender bills, and unspotted underparts. By sight, *M. orientalis* is best distinguished by the small size of its round yellow ear patch, vs. the larger and notably elongated yellow patch of *M. analoga*. Vocally, *M. orientalis* differs in its short snapped downslurred call note, whereas the analogous note of *M. analoga* is a disyllable (not a downslur) with the second note lower pitched. *M. orientalis* also has an upslurred call note, and a musical staccato call *tp* like other meliphagas, and quieter than the *tp* call of Yapen *M. analoga*. Compared to New Guinea mainland *orientalis* populations, that on Yapen differs in its large size (comparable to *M. analoga*, rather than noticeably smaller than *M. analoga* as on the mainland), and in its unspotted, pale grey underparts, unlike the ventral spotting of mainland birds. We found *M. orientalis* common from the summit down to flowering trees at 1,005 m, but replaced by *M. analoga* from around 855 m and below.

WHITE-EARED MELIPHAGA *Meliphaga montana*
Readily distinguished from three of the four other Yapen meliphaga species (*M. orientalis*, *M. analoga* and Puff-backed Meliphaga *M. aruensis*) by its ear patch being clean white rather than yellow; dull dark dorsal and ventral correlation; stout rather than long slender bill; loud wingbeats, unlike not only any other meliphaga but also all other small forest birds in New Guinea; stolid sluggish behaviour; and by not visiting flowering trees. We found it fairly common from the summit to 795 m, from the understorey to the canopy, and usually solitary but for occasionally joining mixed-species flocks. Yawa name: 'markugwá'. The remaining Yapen meliphaga species is Scrub Meliphaga *M. albonotata*, of which KDB saw one in sago swamp forest at sea level in 2016 (the first record for any New Guinea satellite island).

TROPICAL SCRUBWREN *Sericornis beccarii*
Moderately common at 665–1,250 m, being found 1–6 m above ground. Often in mixed flocks with *Gerygone* warblers and *Rhipidura* fantails. The song is a gerygone-like, light, fast, four-note, up-and-down pattern repeated without variation or pause, like a sine wave. Songs of Fairy Gerygone *Gerygone palpebrosa* are confusingly similar, but differ in their slight pauses and alternation of patterns within a song. *S. beccarii* occurs at low elevations (mostly below 1,400 m) on nine outlying mountain ranges (Kumawa, Fakfak, Arfak, Wandammen, Yapen, Van Rees, Foja, Cyclops and North Coastal Range), on north slopes of the Central Range above the Lakes Plains, and south slopes above the Kikori River. Plumage variation among these populations is considerable but geographically irregular, leading to divergent taxonomic treatments (e.g., Mayr 1941, Rand & Gilliard 1967, Diamond 1969, 1985, Beehler & Pratt 2016). Most recently, Beehler & Pratt (2016: 330–333) assigned some populations (including that on Yapen) to Tropical Scrubwren's high-elevation (above 1,400 m) relative Large Scrubwren *S. nouhuysi*. They interpreted the irregular geographic variation as due to variably massive hybridisation between *S. beccarii* and *S. nouhuysi*. We instead consider all low-elevation populations (we have field experience of all 11) to belong to *S. beccarii*, because: they all possess similar songs, distinct from that of *S. nouhuysi*; they all occur at similar elevations up to *c.*1,400 m; none is found above 1,400 m to which all unequivocal *S.*

ISSN-2513-9894 (Online)

nouhuysi populations are confined; and five of them (Kumawa, Arfak, Foja and the north and south slopes of the Central Range) occur sympatrically with high-elevation *S. nouhuysi*, segregating by elevation with *S. beccarii* below and *S. nouhuysi* above 1,400 m. Yawa name: 'punti'?

CHESTNUT-BACKED JEWEL-BABBLER *Ptilorrhoa castanonota*
Observed many times between 665 and 1,110 m in 1983, and at 760–1,135 m in 2017. Our closest sighting was of an individual with blue underparts, wings and superciliary, chestnut upperparts from at least the crown to lower back, and a white throat edged black. Another glimpse was of an individual with chestnut upperparts including the tail. Vocalisations were ones we associate with *P. castanonota* elsewhere: a repeated high note, a duet, and a loud pair of *tsp-tsp* notes, with the second note especially loud. The first record for Yapen.

DIMORPHIC JEWEL-BABBLER *Ptilorrhoa* cf. *geislerorum*
Observed at 440 and 980 m by Verhelst & Pottier (2020).

STOUT-BILLED CUCKOOSHRIKE *Coracina caeruleogrisea*
Seen and heard nine times between 855 and 1,195 m, sometimes in mixed flocks with pitohuis. Yawa name: 'kowat'.

PAPUAN CICADABIRD *Edolisoma incertum*
Common (the most numerous of Yapen's five species of *Coracina* and *Edolisoma*), at 645–1,195 m. Because vocalisations of this species differ dramatically across New Guinea, we mention the three Yapen vocalisations, all shared with both the Foja and Van Rees populations: a series of several dozen buzzy notes repeated on constant pitch, but slightly decelerating; an otherwise similar series of several dozen musical notes repeated on the same pitch (heard only in 1983 but not in 2017); and a cheerful musical staccato call. Yawa name: 'nyukikas'.

HOODED PITOHUI *Pitohui dichrous*
Common from the summit down to 640 m (occasionally 570 m), and overlapping greatly in elevational range with Northern Variable Pitohui *P. kirhocephalus* (summit to sea level). Yapen has the sole insular population of this species. On the New Guinea mainland most populations are montane and largely at elevations above *P. kirhocephalus* or its southern counterpart Southern Variable Pitohui *P. uropygialis*, but *P. dichrous* also has some local populations at sea level. Incessantly before dawn on Yapen, *P. dichrous* repeated its lovely, slow, medium-pitched, signature call of a single note given several times at the same pitch, followed by a lower pitched downslur. Yawa name: 'popok'.

GREEN-BACKED ROBIN *Pachycephalopsis hattamensis*
Our only certain record, and still the only record for Yapen or any satellite island of New Guinea, was of an individual mist-netted at 1,070 m in 1983. Because that individual differs in colour and possibly size from New Guinea populations, it was taken as the type of *P. h. insularis* (Diamond 1985). In 2017 we heard two possible but uncertain calls at 610 and 925 m. The Yapen population must be rare or patchily distributed, because elsewhere the species is common and easily detected by its loud vocalisations.

YELLOW-LEGGED FLYROBIN *Kempiella griseoceps*
Verhelst & Pottier (2020) observed one at 440 m.

ISSN-2513-9894 (Online)

WHITE-RUMPED ROBIN *Peneothello bimaculata*
Our only records were of an individual seen at 900 m and 2–3 m above ground, in 1983, and of an unseen individual singing pre-dawn at 1,195 m in 2017. There were no previous Yapen records, nor on any other island except New Guinea itself.

WHITE-FACED ROBIN *Tregellasia leucops*
In 1983 JD observed six individuals at heights of 3–10 m above ground, and at elevations of 665–1,225 m. We did not encounter it in 2017, and there were no previous Yapen records. However, Verhelst & Pottier (2020) found it common on Yapen's eastern peak above 900 m.

MAGNIFICENT BIRD OF PARADISE *Cicinnurus magnificus*
Modestly common, from the summit down to 535 m, occasionally to 425 m. Females often join pitohuis in mixed-species flocks. Yawa names differ for the sexes, which are totally different in appearance: 'anauput' (male), 'chinchor' (female).

ISLAND LEAF WARBLER *Seicercus poliocephalus*
The commonest singer at 675–1,195 m, often heard in association with mixed-species flocks led by *Gerygone* warblers and *Rhipidura* fantails, but surprisingly infrequently seen. The small size, infrequency of sightings, high altitudinal floor, and the fact that no previous collector except Stein reached its elevational range explain why there were no previous records for Yapen, despite its abundance at high altitudes.

GREEN-FRONTED WHITE-EYE *Zosterops minor*
Common from the summit down to 425 m, in forest and even more numerous in second growth, forming monospecific flocks of up to 20, and occasionally joining mixed-species flocks. Differs from its southern watershed counterpart Black-fronted White-eye *Z. atrifrons* in its lack of a white-eye-ring and of a black forehead. Its song, given persistently before dawn, also differs from the descending 'wheel song' of *Z. atrifrons*: instead, a small but energetic series of notes on the same pitch, ending in 1–3 descending disyllables. Contact calls are weak, but the massed sound of many individuals calling simultaneously in a flock is loud. Yawa name: 'ainami'.

Mixed-species flocks

As elsewhere in New Guinea (Diamond 1987), on Yapen at elevations above 700 m we encountered two types of mixed-species foraging flocks: a 'brown-black' flock of mid-sized omnivores, most with brown and / or black plumage; and a flock of small insectivores. The noisiest, most numerous, and apparently leader species of brown-black flocks were *Pitohui kirhocephalus* and *P. dichrous*. Other regular members were Spangled Drongo *Dicrurus bracteatus*, female-plumaged birds of paradise (*Paradisaea minor*, King Bird of Paradise *C. regius* and Jobi Manucode *Manucodia jobiensis*) and cuckooshrikes (*Coracina caeruleogrisea*, Black Cicadabird *Edolisoma melas*, and *E. incertum*). In small insectivore flocks, the noisiest species were Chestnut-bellied Fantail *Rhipidura hyperythra*, Ochre-collared Monarch *Arses insularis* and Fairy Gerygone *Gerygone palpebrosa*. Other regular members were Northern Fantail *Rhipidura rufiventris*, Rufous-backed Fantail *R. rufidorsa*, Yellow-bellied Gerygone *Gerygone chrysogaster*, *Sericornis beccarii*, *Seicercus poliocephalus*, Grey Whistler *Pachycephala simplex*, Pygmy Longbill *Oedistoma pygmaeum* and Tawny-breasted Honeyeater *Xanthotis flaviventer*.

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